Fig. 2. The form referred to on p. 488; on one side of the specimen the pali are developed, and on the other the calicles are deep and the pali quite obscured as a definite system.

Fig. 3. A form with the more usual ring of five pali. Traces of the others and of the columellar tubercle can be seen.

Fig. 4. A leaf-like specimen of *P. exilis*, Gardiner, showing the directives all pointing in the direction of growth (towards the top edge of the figure).

Fig. 5. A form with thin wavy walls and showing a double calicle; the columellar tangle rises to the surface, and here and there unites the pali in a ring.

Fig. 6. A cœnenchymatous form, the cœnenchyma rising into rounded ridges and papillæ; the pali are slightly exsert and are often slightly V-shaped. In a few cases the directive principal and its adjacent lateral supplementaries can be seen forming a very blunt broad arrow (the triple fusion mentioned on p. 490).

The Air-bladder and its Connection with the Auditory Organ in *Notopterus borneensis*.

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[Read 21st December, 1899.]

(Plates 36 & 37.)

Contents.

I. Introduction.

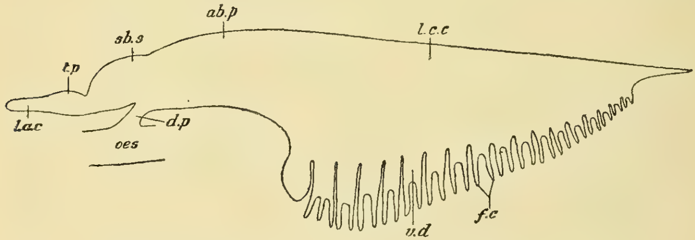
While recently dissecting the air-bladder and associated structures in a specimen of *Notopterus borneensis*, Bleeker, certain features were noticed in which this species differed from *Notopterus Pallasii*, C. & V., as described by Cuvier and Valenciennes (4. pp. 139–141). How far the differences observed are due to imperfections in the account given by the two distinguished French zoologists whose names have been mentioned, or to the existence of genuine variations in which *N. borneensis* deviates from *N. Pallasii*, I am not in a position to decide. Nevertheless, and apart from the question of specific variations in the structure of a particular organ, there are other features in the air-bladder of *N. borneensis*, and more especially its connection with the auditory organ, which, perhaps, are not without importance to those interested in the study of the obscure but fascinating problem of subaqueous audition. For these reasons I venture to give a brief account of the air-bladder of *N. borneensis*, and, as the organ has not hitherto been figured in any species of the family, to supplement the description by suitable figures.

I desire to express my grateful thanks to the Council of the Royal Society for a grant from the Research Fund in aid of this and other kindred investigations.

II. The General Structure and Relations of the Air-bladder.

The specimen examined was 38 cm. long, and to this length the postanal portion of the body or tail contributed 28 cm.

For convenience in description, the air-bladder may be said to consist of three well-defined portions, which, from their regional disposition, may be termed (1) the anterior or pre-cœlomic, (2) the abdominal or cœlomic, and (3) the caudal or post-cœlomic.



Lateral view of the air-bladder of *Notopterus borneensis*. About two-thirds nat. size. *ab.p*, abdominal portion; *l.c.c*, left caudal cæcum; *d.p*, ductus pneumaticus; *f.c*, filiform cæca; *l.a.c*, left auditory cæcum; *œs*, œsophagus; *sb.s*, subspherical sac; *t.p*, its tubular prolongation; *v.d*, ventral diverticulum.

The abdominal portion (see fig., *ab.p.*) is more or less cylindrical in shape, but much deeper behind than in front, and occupies the usual position beneath the vertebral column, being separated from the latter by the kidney. The ventral surface only is invested by the peritoneum, the line of reflection of this membrane on to the inner surface of the abdominal wall being coincident with the junction of the lateral with the ventral wall of the organ. Posteriorly, the peritoneum is reflected downwards on to the hæmal arch and spine of the first caudal vertebra and the first radial element ("interspinous bone" or "pterygiophore") of the anal fin, and therefore does not accompany the caudal prolongations of the air-bladder.

At its hinder extremity, immediately anterior to the first radial element of the anal fin, the abdominal portion of the bladder divides into two caudal cæca (*l.c.c.*), each of which at its commencement, if not so wide, is nearly twice the vertical dimension of the former. The two cæca extend backwards on opposite sides of the tail, and, gradually contracting, finally terminate in pointed and almost filiform extremities about 13 cm. behind the anus, or, approximately, about the middle of the length of the tail. In its course along the tail each cæcum is situated wholly internal to the caudal musculature of its side, and in immediate contact with the hæmal spines of the caudal vertebræ and the supporting radial elements of the extensive anal fin. The dorsal and external walls of each cæcum are invested by a strong aponeurotic membrane, the outer surface of which receives the insertions of the inner margins of the fibrous septa separating the caudal myotomes.

Along nearly the whole length of each of the caudal prolongations of the air-bladder, the ventral margin gives off a fringe of numerous short but relatively wide diverticula (*v.d.*), which form pairs with their fellows of the opposite side of the tail. With the exception of the first two of the series, each diverticulum eventually terminates by subdividing into an anterior and a posterior slender, filiform cæcum (*f.c.*), which extend ventrally towards the base of the anal fin, and are intercalated between, and partially covered by, the superficial flexor muscles of the contiguous dermal fin-rays, but are external to the corresponding deep flexors. The second diverticulum has three filiform cæca, while the first remains simple and undivided. The series of ventral diverticula and their filiform prolongations gradually diminish in size from before backwards, and eventually cease at some little distance anterior to the tapering terminal portions of the caudal extensions of the bladder.

The anterior or pre-cœlomic section of the air-bladder consists posteriorly of a somewhat subspherical sac (*sb.s.*), separated externally from the abdominal portion of the organ by a shallow transverse or obliquely disposed groove. In this groove the subvertebral portion of the mesonephros curves downwards on each side to fuse with the large anterior and unpaired portion of that organ, or "head-kidney," which is situated dorsad to the heart and gills, but ventrad to the subspherical sac. Anteriorly, the sac abruptly contracts to form a somewhat tubular or slightly inflated, median prolongation (*t.p.*), which extends forwards immediately above the dorsal extremities of the hinder branchial arches, in contact with the ventral surfaces of the centrum of the first vertebra and the basioccipital, and by each of its lateral surfaces is in relation with the branchial branches of the corresponding pneumogastric nerve. A constriction separates the subspherical sac from its tubular prolongation, and at the same time transmits on the left side the cœliac branch of the dorsal aorta. Eventually the tubular prolongation divides into two somewhat narrower, cæcal, auditory cornua, each of which (*l.a.c.*) diverges somewhat from its fellow and passes upwards and outwards, as well as forwards, in order to reach the outer surface of the auditory capsule of its side, where, as Cuvier and Valenciennes (*op. cit.* p. 140) have described in the case of *Notopterus Pallasii*, it becomes intimately associated with the enclosed membranous labyrinth of the organ of hearing. Between the origins of the two auditory cæca, and on the dorsal side, the dorsal aorta may be seen passing backwards to reach the bony aortic groove, to which further reference will subsequently be made.

The whole of the anterior section of the air-bladder is situated in front of the abdominal cavity, and consequently none of its various divisions or chambers are invested externally by the peritoneum.

It is perhaps worthy of note that anteriorly and dorsally the branchial cavity is prolonged forwards on each side of the skull for some distance, parallel to the lateral surface of the auditory capsule, and directly external to the corresponding auditory cornua of the air-bladder. This singular extension of the branchial cavity practically takes the form of a cæcal diverticulum (Pl. 36. fig. 1, *a.b.c.*), ending blindly in front by reason of the gradual contraction of its walls, but communicating behind with the general branchial cavity. Into each cæcal diverticulum the dorsal portions of the first and second branchial arches (*br.*[1], *br.*[2]), with their branchial lamellæ, extend for some distance; the remaining arches, however, lying posterior to the opening of the diverticulum into the dorsal portion of the branchial cavity. The relatively thin inner wall of the branchial diverticulum is coextensive with, and directly and closely invests the outer wall of, the corresponding auditory cæcum (*l.a.c.*), and hence in this region the air-bladder and its gaseous contents are more intimately related to the external medium in which the Fish lives than is the case at any other point.

For a Teleost the ductus pneumaticus (text-fig., and Pl. 36. fig. 3, *d.p.*) is remarkably short and unusually wide, its length not exceeding 3 mm., while its lumen, even in a spirit-preserved specimen, is approximately the same in diameter. The œsophageal opening of the ductus is in the mid-dorsal line, and about 8 mm. behind the last branchial cleft. The aperture by which the ductus communicates with the air-bladder is situated a little to the left of the median ventral line, and directly posterior to the oblique groove (*o.g.*) separating the subspherical sac from the abdominal portion of the organ. The ductus is surrounded at its œsophageal extremity by a strong sphincter muscle, but no valvular mechanism in connection with either of its apertures could be detected.

No gas-secreting or gas-absorbing "red-glands" or "red-bodies" were to be found in the air-bladder.

III. The Internal Structure, and the Relations and Attachments of the Air-bladder to the Skeleton.

In the condition of their inner or mesial walls, and in the relation of these structures to the skeletal elements of the tail, the caudal prolongations of the air-bladder present several interesting features.

With regard to the character and disposition of the caudal skeletal elements, it may be mentioned that the hæmal spines of the suprajacent vertebræ are relatively short (Pl. 36. fig. 2, *h.s.*). The radial elements of the anal fin (*r.e.*), on the contrary, are of considerable length in the anterior part of the tail, although they gradually become much shorter as they are traced backwards towards the caudal fin; and as two of them, forming a pair, are associated dorsally with each hæmal spine, it follows that the radial elements are twice as numerous as the caudal vertebræ, at any rate in the region of the air-bladder. At the commencement of the tail only the ventral third of the radial elements serve for the origin of the flexor muscles of the anal fin-rays, the dorsal two-thirds, and the short hæmal spines with which the former interdigitate, being quite free from muscular attachment. With the gradual shortening of the radial elements towards the middle portion of the tail, where the air-bladder terminates, nearly the whole length of each radial element becomes invaded by the origin of the flexor muscles. The area over which the various radial elements are wholly devoid of muscular attachment is coextensive with that of the inner wall of each of the two closely-related caudal cæca. The series of radial elements and hæmal spines are connected together by a thin, but tough, sheet of fibrous tissue, which extends from one to the other and fills up the intervals between them, and, with the caudal skeletal elements above mentioned, form the only separation between the caudal cæca of opposite sides of the tail. It may be added, that the series of ventral diverticula occupy the intervals between the successive pairs of radial elements.

The dorsal and outer walls of each caudal cæcum are of moderate thickness, as also are the external walls of the ventral diverticula, while the filiform cæca have much thinner walls. In each case, nevertheless, a relatively thick outer fibrous stratum or tunica externa, and an extremely thin lining or tunica interna, consisting of an internal epithelial stratum, supported externally by a thin layer of connective tissue, can readily be recognized. The inner wall of each caudal cæcum, including also that of each of its primary ventral diverticula, on the contrary, is of extreme tenuity, consisting only of the tunica interna, and, moreover, is closely adherent to the outer surfaces of the radial elements and hæmal spines, and also to the fibrous sheet which stretches between them. In fact, in the intervals between these skeletal elements, the median fibrous sheet and the attenuated inner walls of the caudal cæca are all that separate the cavities of the cæca of opposite sides of the tail; and so thin are the inner walls of these that, when the cavity of either of them is exposed by the removal of its outer wall, the various skeletal elements (*h.s.*, *r.e.*) appear as if completely bare of any investing tissue and to project freely into the lumen of the bladder.

In addition to the investment of the outer surfaces of the caudal skeletal elements by the tunica interna of the inner wall, the dorsal and ventral walls are also firmly attached to the skeleton. Along its inner or mesial dorso-lateral margin, where the relatively thick dorsal wall becomes continuous with the attenuated inner wall, the tunica externa becomes somewhat thickened and terminates by becoming firmly attached to the bases of the hæmal spines and also to the dorsal extremities of the two radial elements with which each spine is associated. Ventrally also the tunica externa thickens and forms a series of strong transversely disposed ridges projecting from the floor of the cæcum, and separating the orifices leading into the ventral diverticula. Traced towards the inner wall of the cæcum, the ridges cease by becoming inserted into the adjacent sides of two contiguous radial elements and to the connecting fibrous membrane which extends between them. On the other hand, if traced ventrally, the fibres of each ridge split to form the posterior wall of one diverticulum and the anterior wall of the next succeeding diverticulum, both walls nevertheless retaining their mesial attachments to the contiguous radial elements between which the diverticulum is situated.

Near the dorsal wall of each caudal cæcum, the fibrous sheet between the radial elements presented a series of oval vacuities (*d.v.*), which were disposed in regular order between the successive pairs of radial elements which are attached to the vertebral hæmal spines. Over most of these vacuities the thin inner wall of the caudal cæcum appears wanting, and hence the cavity of each cæcum seems to communicate with that of its fellow at these points. In one or two instances, however, it is clear that no such communication exists, for, notwithstanding the vacuity in the fibrous sheet, the opposed inner walls of the two cæca remain intact over the area of the vacuity. It is difficult, therefore, to be quite certain that these vacuities are associated with normal perforations in the opposed walls of the cæca, or that the cavities of the latter really intercommunicate during life, or in perfectly fresh specimens, more especially as, owing to its thinness and fragile character, the tunica interna is extremely likely to break down and disintegrate where unsupported by the much stronger and more resistant fibrous sheet, unless more than ordinary care is taken with the preservation of the Fish.

A similar series of small, oval, or rounded vacuities (*v.v.*) in the interradial fibrous membrane was also present towards the ventral side of each caudal cæcum, where the membrane in question separates the closely related inner walls of the two series of ventral diverticula, and, as regards their relations to the caudal skeleton elements, these correspond in position with the dorsal series. Wherever these ventral vacuities existed, corresponding perforations in the opposed inner walls of the diverticula were also present, and each of the latter seemed to communicate with its fellow of the opposite side of the tail. In some instances it was possible to determine the continuity of the inner wall of a diverticulum with the corresponding wall of its fellow at the edges of the vacuity ; and for this reason I am inclined to believe that the caudal cæca are really in communication with each other ventrally, through the fusion and subsequent perforation of the inner walls of their ventral diverticula. Nevertheless, it is perhaps desirable that the caution needful in the case of the apparent dorsal perforations should also be observed here, at all events until fresh or well-preserved specimens of *Notopterus* have been submitted to examination.

A somewhat interesting numerical and regional correspondence is to be observed in the anterior half of the tail between the various caudal skeletal elements and the arrangement of the cæcal outgrowths from the caudal divisions of the air-bladder.

Thus, the ventral diverticula are situated exactly opposite the intervals between the series of hæmal spines, and, at the same time, occupy the interspaces between successive pairs of radial elements ; that is, each diverticulum fills up the interval between two contiguous pairs of radial elements which, dorsally, are attached to the hæmal spines of two successive caudal vertebræ. Hence, therefore, the diverticula closely agree in number with the pairs of radial elements, and in position may be said to be intervertebral. Again, each of the series of fibrous ridges which separate the orifices of communication between the ventral diverticula and the caudal cæca, is attached to the opposed surfaces of a pair of radial elements as well as to the fibrous membrane between them ; and as each ridge coincides dorsally with the hæmal spine to which the two radial elements belong, it is vertebral in its relations to the axial skeleton. Lastly, the filiform cæca agree in number with the radial elements, the posterior cæcum of one diverticulum, and the anterior cæcum of the next succeeding diverticulum, being situated immediately external to the corresponding factors of two contiguous pairs of radial elements.

The dorso-lateral margins of the abdominal portion of the air-bladder (Pl. 36. fig. 3) are firmly attached to the transverse processes of certain of the trunk vertebræ and to the proximal portions of their costal elements, the latter being so intimately related to the bladder as to produce a series of faint transversely-disposed grooves in the lateral walls of that organ. As previously stated, the peritoneum invests the ventral surface of this portion of the air-bladder; and it may be added, that in this region it assumes the condition of an exceptionally tough fibrous membrane which is firmly adherent to the ventral wall of the bladder. Posteriorly, the peritoneum is reflected downwards on to the hæmal arch and spine of the first caudal vertebra and the first radial element of the anal fin, and is, moreover, firmly attached to these skeletal structures. Hence it follows, that the ventral wall of the abdominal section of the air-bladder is firmly attached posteriorly to the anterior caudal skeletal elements. The walls of this portion of the bladder are of moderate and equal thickness throughout. Internally, the cavity of the bladder is subdivided into two lateral compartments by a vertical longitudinal septum, which is continuous dorsally and ventrally with the corresponding walls of the bladder (fig. 3, *l.s.*). Posteriorly, the septum increases in height with the increasing vertical dimension of the bladder, and, at the point where the latter subdivides into the two caudal cæca, the hinder margin of the septum is inserted into the anterior face of the hæmal arch and spine of the first caudal vertebra and the proximal portion of the first radial element of the anal fin. Anteriorly, the longitudinal septum deviates from the median plane towards the left side, and, so far as its ventral portion is concerned, the septum ceases immediately behind and a little to the right side of the internal aperture of the ductus pneumaticus (*l.s.*, *d.p.*). At this point the dorsal portion of the septum, which, it may be mentioned, extends forwards into the subspherical sac, is connected by a narrow obliquely-transverse septum (*t.s.*) with the left lateral wall of the bladder along the line of the external oblique groove (*o.g.*) separating the sac from the abdominal portion of the bladder*. The effect of this singular unsymmetrical disposition of the longitudinal septum, and the presence of an oblique transverse septum on the left side only, combined with the

* In fig. 3 that portion of the left lateral wall of the bladder which is traversed by the oblique groove is indicated as a slender strip.

position of the aperture of the ductus pneumaticus slightly to the left of the median line, is (1) that the left lateral compartment is smaller than the right; (2) that the orifice of communication between the subspherical sac and the left lateral chamber is reduced to the condition of a relatively small aperture, which is in striking contrast to the widely open, direct communication between the sac and the lateral compartment of the right side; and (3) that while the ductus pneumaticus opens directly into the left compartment, its connection with the right chamber is somewhat indirect and takes place through the cavity of the subspherical sac, round the free anterior margin of the ventral portion of the longitudinal septum (fig. 3).

Like the abdominal portion of the bladder, the subspherical sac (Pl. 36. fig. 3, *sb.s.*) is firmly attached along its dorso-lateral margins to the transverse costiferous processes of certain of the trunk vertebræ, viz., the second to the fifth, inclusive. Its dorsal wall is extremely thin, and, in fact, is represented by the tunica interna alone; the latter stratum, in the absence of the mesonephros in this region, being closely adherent to the lateral and ventral surfaces of the anterior vertebral centra. Internally, the sac is partially subdivided by an extremely thin median longitudinal septum (*l.s.'*), which projects downwards from its dorsal wall, and is a direct continuation of the dorsal half of the longitudinal septum previously mentioned as unsymmetrically dividing the cavity of the abdominal portion of the air-bladder. The septum is best developed behind, and gradually diminishes in height towards the anterior limit of the sac. Its free ventral margin is remarkably thick and forms a strong, arch-like band, the fibres of which diverge behind to strengthen and stiffen the inner and outer lips of the orifice by which the sac communicates with the left lateral compartment of the preceding portion of the bladder. Anteriorly also the band divides, but into three fibrous bundles, the more laterally-situated of which diverge downwards into the lateral walls of the sac and strengthen the outer lips of the aperture through which the sac communicates with its anterior tubular prolongation, while the mesial fibres continue their forward course.

IV. Relations of the Air-bladder to the Skull and Auditory Organs.

The structure of the tubular prolongation of the subspherical sac and of the auditory cæca, and the relations of both to the skull and the auditory organ, will be better understood after a brief description of certain structural features in connection with the hinder part of the skull (Pl. 37. fig. 4).

The basioccipital (*b.o.*) is somewhat hourglass-shaped, being slightly constricted at the junction of the hinder third with the anterior two-thirds of its length, and expanded towards either extremity, but much more so in front than behind. The hinder half of the bone is produced ventrally into a laterally-compressed bony keel, which is traversed by a moderately deep, median, longitudinal groove, bounded by prominent lateral ridges, and transmitting the initial section of the dorsal aorta.

Traversing the lateral surface of the basioccipital, immediately ventrad to the sutural articulation of this bone with the exoccipital and opisthotic, is a well-marked oblique ridge, which, on each side, extends backward and downward and finally terminates in a free projecting process (*a.p.*), closely applied to the ventro-lateral surface of the centrum of the first vertebra after the fashion of an accessory articular process. Between the aortic groove ventrally and the oblique ridge dorsally, the lateral surface of the basioccipital is traversed by a fairly deep groove (*b.g.*), the direction of which is obliquely upward and forward towards the outer surface of the auditory capsule of the same side. Anteriorly to the commencement of the aortic groove the basioccipital ceases to be laterally compressed, and, instead, becomes greatly swollen laterally, assuming in fact a distinctly bullate appearance. The lateral surface of this portion of the bone is also traversed by a well-defined groove, which, however, is merely an extension forwards of that mentioned above. Ventrally, the anterior half of the basioccipital is in relation with the hinder portion of the parasphenoid (*ps.*), and in front the bone articulates by means of an irregular squamous suture with the hinder margin of the prootic (*pro.*).

There is a complete series of periotic bones, which, in the main, exhibit the usual relations one to another and to the adjacent cranial bones. The opisthotic (*op.*) forms the postero-lateral portion of the auditory capsule, articulating with the exoccipital (*eo.*) behind, the pterotic (*pt.*) above, with the supero-lateral margin of the basioccipital (*bo.*) below, and in front with the prootic (*pro.*). The relatively large prootic (*pro.*) forms the anterior portion of the periotic capsule, and articulates above with the sphenotic (*spo.*) and pterotic (*pt.*), below with the parasphenoid (*ps.*), and posteriorly and dorsally with the opisthotic (*op.*), while the posterior portion of the bone forms a thin squamous lamina which extends backwards, overlapping the lateral surface of the basioccipital (*bo.*), and at the same time closing in the anterior portion of the basioccipital groove. In addition, the ventral portion of each prootic sends inwards a strong horizontal process (Pl. 37. fig. 5, *pro.*), which unites with its fellow in the floor of the cranial cavity behind the pituitary fossa. The pterotic (Pl. 37. fig. 4, *pt.*) constitutes the superior lateral margin of the auditory capsule, and also contributes the usual articular surface for the proximal extremity of the hyomandibular; anteriorly, the bone is in articular relation with the upper surface of the prootic and with the sphenotic, and behind overlaps the dorsal margin of the opisthotic. The sphenotic (*spo.*) is a small nodular ossicle, wedged in between the upper margin of the prootic and the overlapping anterior extremity of the pterotic.

As already indicated, the anterior termination of each lateral basioccipital groove is overlapped by the squamous posterior extension of the prootic, and thus becomes converted into a short, but relatively spacious, bony cul-de-sac (*c.s.*), continuous behind with the open portion of the groove, but terminating blindly in front. The inner or cranial wall of the cul-de-sac is coincident with a somewhat considerable fontanelle (Pl. 37. fig. 5, *a.f.*), which is encircled above, below, and in front by the prootic (*pro.*), and behind is limited by the anterior margin of the opisthotic (*op.*) and by the antero-superior border of the basioccipital (*bo.*), and in the dried skull places the cul-de-sac in free communication with the cavity of the auditory capsule. The formation of this auditory fontanelle is apparently due to the widening of the normal sutures which separate the surrounding periotic elements one from another and from the basioccipital. An extremely thin fibrous membrane, which in texture, colour, and appearance closely resembles the membrane closing the supero-lateral cranial fontanelle, extends between the margins of the auditory fontanelle, and constitutes the only separation between the lumen of the bony cul-de-sac and the perilymph-containing cavity of the auditory capsule.

Returning now to the air-bladder (Pl. 36. fig. 3), it may be stated that the dorsal surface of the tubular prolongation (*t.p.*) of the subspherical sac is closely moulded to the ventral surface of the centrum of the first vertebra, and also to the ventral and lateral surfaces of the hinder part of the basioccipital. From its laterally-compressed shape, the ventral portion of the latter bone forms a median keel projecting downwards and pushing before it the dorsal wall of the subjacent part of the air-bladder, which, consequently, appears as if partially subdivided internally by an incomplete, but very thick, longitudinal partition (*l.p.*), while dorso-laterally the bladder fills up the grooves on the lateral surfaces of the basioccipital. Laterally and ventrally, this portion of the air-bladder is free from any special relations or attachments to the skeleton, and hence its moderately thick walls consist of both tunica externa and tunica interna: elsewhere, however, the walls are intimately related to the skeleton, and then are either firmly attached thereto or become greatly reduced in thickness. Thus, dorso-laterally, on each side, the tunica externa ceases by becoming inserted into the oblique bony ridge on the lateral surface of the basioccipital. In the mid-dorsal line, the tunica externa is not only considerably thickened by mesial fibres derived from the arch-like band which forms the free ventral margin of the longitudinal septum of the subspherical sac, but is also attached to the lips of the bony aortic groove in such a way as to convert the groove into a canal. Between the mid-dorsal and the dorso-lateral skeletal attachments, however, the tunica externa is wanting, and all that represents the proper wall of this part of the bladder is the thin tunica interna investing and lining the hinder portion of the grooves on the lateral surfaces of the basioccipital, into which the lateral portions of the bladder are received. The diameter of the tubular portion of the bladder is about 6 mm.

The two auditory cæca (*l.a.c.*, *r.a.c.*) communicate with the preceding part of the bladder by relatively wide orifices; and at this point the simple non-septate lumen of each cæcum is about 3·5 mm. in diameter. From their origins the two cæca diverge obliquely upward and forward towards the outer surfaces of their respective auditory capsules. In its forward extension, each auditory cæcum traverses the anterior portion of the oblique groove on the lateral surface of the basioccipital, and, with only a slight reduction in calibre, appears to terminate at the sutural junction of the latter bone with the prootic. The outer lateral wall of each cæcum is complete, but both dorsally and ventrally its tunica externa ceases by becoming firmly inserted into the corresponding lips of the basioccipital groove in which the cæcum is lodged. Towards the anterior termination of the cæcum even the tunica externa of the outer wall disappears through its continuity with the hinder margin of the prootic bony lamina, which, anteriorly, converts the groove into a cul-de-sac. The inner wall, on the contrary, is throughout formed by the tunica interna alone, and, moreover, is closely adherent to the sides of the basioccipital groove.

Reduced to a simple wall of tunica interna of extreme tenuity, the terminal portion of the auditory cæcum now enters the bony cul-de-sac (Pl. 37. fig. 4, *c.s.*), and, on its inner or cranial side, becomes closely applied to the outer surface of the membrane closing the auditory fontanelle (fig. 5, *a.f.*).

V. The Cranial Fontanelles and their Relation to the Auditory Organ.

In their account of the bones of the skull in *Notopterus Pallasii*, Cuvier and Valenciennes (4. p. 143) describe two interesting vacuities in the postero-superior aspect of the cranial roof. "Ces mastoïdiens ont en avant une très-profonde échancrure, qui cerne près des deux tiers du grand trou pariéto-mastoïdien, dont les côtés du crâne sont percés, une échancrure du frontal postérieur contribue aussi à former le cercle de ce trou. Ce grand trou, analogue à celui que nous avons observé dans l'Alose et dans plusieurs autres Clupées, mais beaucoup plus semblable encore à ce que existe dans le Mormyre, est bouché par une couche peu épaisse de cette mucosité graisseuse, qui remplit les cavernes du crâne et sur laquelle passe la peau mince, nue et sans écailles de la tête. Par ce trou on pénètre largement dans l'intérieur de la cavité du crâne, et l'on voit presque sans dissection, après avoir toutefois enlevé toutes ses parties externes, les canaux semicirculaires supérieurs, leur ampoule commune et une portion du sac qui contient l'otolithe."

This description is in the main an accurate one, but may nevertheless be supplemented in certain details.

Two longitudinal grooves traverse the lateral portions of the cranial roof, and are bounded for the anterior part of their extent by prominent bony ridges on the external surface of the frontals, and more posteriorly by similar parallel ridges on the upper surface of the pterotic (Pl. 37. figs. 4 & 6, *g*). Externally, the grooves are closed in and converted into complete canals by the thin, scaleless, superficial skin of the dorsal surface of the head. In these grooves or canals are lodged the main lateral sensory canals of the head and their respective supra-orbital prolongations. At its hinder extremity each groove suddenly deepens into a shallow basin-shaped, or funnel-like, oval depression, at the bottom of which is the somewhat smaller, but also oval, cranial fontanelle (Pl. 37. fig. 6, *c.f.*), which in the dried skull communicates internally with the cavity of the auditory capsule, precisely as described by Cuvier and Valenciennes. The margins and sides of the funnel are smooth and rounded, and are formed anteriorly, and also to a large extent on each side, by the deeply concave posterior border of the pterotic (*pt.*), and completed laterally and behind by the epiotic (*ep.*), the opisthotic (*op.*), and the exoccipital (*eo.*). The long axis of the mouth of the funnel measured 10 mm., and its transverse dimension 6 mm. The fontanelle is smaller, the corresponding dimensions being 6 mm. and 4 mm. respectively. Across the fontanelle, and firmly attached to its margins, is stretched a thin, fibrous, drum-head-like membrane, which is in relation internally with the somewhat fatty perilymphatic tissue of the interior of the auditory capsule.

There is, however, one point to which Cuvier and Valenciennes make no reference, viz.—the relations of the main sensory canal of the head to the cranial fontanelle and the membrane closing it. As it passes directly dorsad to the proximal or supra-clavicular element of the pectoral girdle, the sensory canal traverses the axis of a somewhat cylindrical bone, and then enters the lateral longitudinal groove or canal to which reference has just been made. At this point the sensory canal expands considerably, and assumes a singular cavernous or sinus-like appearance, practically filling the bony groove in which it is lodged. The lateral and inner walls of the sensory canal are here strengthened by two longitudinally-arranged, thin, demi-cylindrical bones, or sensory canal ossicles, the convex inner surfaces of which are in close relation with the cranial fontanelle and the whole extent of the outer surface of its drum-head membrane, while the outer wall of the sensory canal is in contact with the external scaleless skin of this part of the head.

Practically, therefore, the cavernous sensory canal and its investing ossicles completely separate the cranial fontanelle and its membrane from the superficial skin. Anteriorly to the fontanelle the sensory canal is still of considerable width, but, as it passes dorsad to the orbital cavity, gradually contracts to more normal dimensions.

VI. The Auditory Organ.

The utriculus and the sacculus of each side occupy a spacious common recess excavated in the substance of the corresponding lateral half of the large basioccipital (Pl. 37. fig. 5, *u.s.r.*). So large is the recess, that the outer portion of nearly the anterior two-thirds of the bone is reduced to the condition of a thin partially transparent shell, and corresponds to the externally bullate portion to which reference has already been made; while a thin, vertical, bony partition in the axis of the basioccipital is all that separates each recess from its fellow of the opposite side of the skull. The two recesses are partially roofed in by the mesial union of horizontal ingrowths from the two opisthotic bones (*op.*), in a fashion which recalls the method by which the similarly-situated saccular recesses are roofed by the exoccipitals in the Siluroid Fishes. The utriculus occupies the anterior two-thirds of the utriculo-saccular recess, and is relatively of large size. The much smaller sacculus fills up the hinder third of the recess, and is connected with the utriculus by a very short but obvious ductus sacculo-utricularis. Anteriorly and dorsally, the utriculus gives off a conical, forwardly-directed diverticulum, which occupies a recess of corresponding shape excavated in the prootic *. Near the origin of the diverticulum, the ampullary extremities of the horizontal and the anterior vertical semicircular canals communicate with the utriculus by opening into a small recessus utriculi. The great utricular otolith, or "sagitta," is nearly as large as the cavity of the utriculus itself; and it is interesting to note that, anteriorly and dorsally, the otolith is produced into a conspicuous, tapering, conical process, which extends into the

* *Cf.* Ridewood's account of the auditory organ in the Clupeidæ (9).

utricular diverticulum in the prootic. The membrane which closes each auditory fontanelle (*a.f.*), and is invested externally by the tunica interna of the auditory cæcum of the air-bladder, is almost in contact internally with the outer wall of the utricular diverticulum. The semicircular canals have the normal arrangement, both as regards their relations to the utriculus and to the various periotic bones. It may be mentioned, however, that each supero-lateral cranial fontanelle (*c.f.*) is almost completely encircled by the three semicircular canals—the horizontal canal in the pterotic (*pt.*) curving round the lower or outer border, the posterior vertical canal in the epiotic (*ep.*) and opisthotic (*op.*), and the anterior vertical canal in relation with the inner surface of the prootic (*pro.*), being similarly situated with regard to the anterior and hinder margins respectively; while the vertically-disposed common stem, or sinus utriculi superior, by which the two latter canals join the utriculus, crosses the fontanelle at a short distance internal to the membrane which closes it.

Careful examination failed to reveal the existence of any connection between the sacculi of opposite sides by means of the supra-cerebral or sub-cerebral union of their endolymphatic ducts, such as has been described by Weber (12) for *Silurus glanis*, and in the case of other Siluroids by Bridge and Haddon (2) and Ramsay Wright (13), and by Hasse (6) for the Herring (*Clupea harengus*); or of any communication between the two utriculi, similar to the sub-cerebral connection which has been described in the last-mentioned Teleost by Weber (12), and in the Shad (*Clupea alosa*) by Breschet (1). It must be admitted, however, that the single specimen of *Notopterus* examined by me was not sufficiently well-preserved to quite justify purely negative conclusions on these points.

VII. Comparison with *Notopterus Pallasii*.

As regards the general structure and relations of the various divisions of the air-bladder, the account above given agrees generally with that of *N. Pallasii* by Cuvier and Valenciennes. In certain details, however, there are important discrepancies, which may be due either to the existence of structural variations in the two species, or possibly to errors in the description of the air-bladder of *N. Pallasii*. The more important of these differences will now be considered.

In their account of the air-bladder of *N. Pallasii,* Cuvier and Valenciennes (4. pp. 139–141) make no mention of the existence of a series of branched diverticula similar to those which fringe the ventral margins of the caudal prolongations of the air-bladder in *N. borneensis*; neither do these authors refer to the extreme tenuity of the inner walls of these portions of the bladder, or to their attachments and relations to the caudal skeletal elements, nor to the existence of vacuities in the closely related inner walls of the caudal cæca, by which the cavities of the two cæca freely intercommunicate.

In their description of the caudal portion of the bladder in *N. Pallasii*, Cuvier and Valenciennes (*op. cit.* p. 139) remark :— "Il existe sur la surface externe des cornes un organe singulier, comme glanduleux, divisé par un nombre considérable de filets blanchâtres, anastomosés entre eux en petits lobules, que l'on ne pourrait séparer par la dissection qu'avec beaucoup de peine. Cet organe, qui couvre presque tout le bas de la corne, ne dépasse guère la moitié de sa longueur."

No trace of any such gland-like structure could be detected in *N. borneensis* ; and as no organ of a similar character is known to be associated with the external surface of the air-bladder in any other Fishes, it is impossible to hazard even a conjecture as to its nature in *N. Pallasii.*

In their description of the abdominal and anterior portions of the air-bladder, Cuvier and Valenciennes apparently failed to note the skeletal attachments of the organ, or the general tendency of the bladder to lose its external fibrous coat wherever its walls enter into intimate relations with the cranial or vertebral elements of the skeleton. The unsymmetrical subdivision of the abdominal section of the bladder seems also to have escaped their notice.

The account given by Cuvier and Valenciennes of the mode of termination of the auditory cæca and their relations to the membranous labyrinth in *Notopterus Pallasii* is so different from my own observations on *Notopterus borneensis,* that I venture to quote their remarks *in extenso.*

After describing the extension of the air-bladder towards the cranium, it is stated : " De là elle donne deux cornes qui s'engagent dans l'intérieur de la boîte cérébrale sous les mastoïdiens, en passant entre l'os et le sac de l'oreille. Ces cornes s'avancent dans l'intérieur de la boîte cérébrale jusque sur la grande aile du sphénoïd, et atteignent la hauteur de la scissure qui sépare le second tubercule, ou le tubercule optique du cerveau, du troisième, derrière lequel existe le cervelet. En pénétrant dans la boîte cérébrale la vessie perd ses tuniques fibreuses, ou plutôt c'est la seule tunique propre ou membraneuse de la vessie qui s'avance ainsi dans la cavité du crâne. On voit en dedans de la corne le sac qui contient la pierre de l'oreille. Il y a donc ici communication médiate entre la vessie et l'organe de l'ouïe; c'est le seul exemple que je connaisse d'une communication aussi intime entre la vessie et l'organe de l'ouïe" (*op. cit.* p. 140).

It is quite certain that the auditory cornua or cæca do not enter the cranial cavity in *N. borneensis*, but, on the contrary, are wholly extra-cranial. The statement quoted above that "en pénétrant dans la boîte cérébrale la vessie perd ses tuniques fibreuses, ou plutôt c'est la seule tunique propre ou membraneuse de la vessie qui s'avance ainsi dans la cavité du crâne," correctly describes the behaviour of the auditory cæca on entering the bony culs-de-sac in which their terminal extremities are lodged; and it is therefore possible that Cuvier and Valenciennes have mistaken this canal for a portion of the cranial cavity. It has been shown, however, that this canal has no communication with the cranial cavity, inasmuch as it remains separated therefrom either by the thin membrane which closes the auditory fontanelle, or by the various periotic bones surrounding it. Hence it follows that the subsequent statement, "Il y a donc ici communication médiate entre la vessie et l'organe de l'ouïe," is obviously erroneous as regards *Notopterus borneensis*, whether it implies an open communication between the two organs, or the existence of a direct connection by the simple apposition of their limiting walls; and I entertain little doubt that the statement is equally inapplicable to *Notopterus Pallasii.*

It is also stated by Cuvier and Valenciennes that *Notopterus* affords the only instance known to them "d'une communication aussi intime entre la vessie et l'organe de l'ouïe; car je n'hésite pas à répéter ici que celle qui avait été annoncée dans l'Alose ou dans le Hareng, et dans plusieurs autres poissons, n'existe réellement pas" (*op. cit.* p. 140).

The reference to the Allis Shad (*Clupea alosa*) and the Herring (*C. harengus*), as Ridewood (9. p. 40) has pointed out, is evidently based on the misconception that previous writers had described an open communication between the air-bladder and the auditory organ, such as Valenciennes apparently believed to exist only in *Notopterus*. It is now scarcely necessary to add that no such open communication exists, or has even been affirmed to exist, in any Fish except *Notopterus Pallasii*; and, for the reasons given above, it is extremely improbable that the latter species offers any exception to the general rule, or, so far as this point is concerned, differs in any way from its congener, *Notopterus borneensis*.

VIII. Comparison with other Teleosts.

Perhaps the most interesting point in the air-bladder of *Notopterus* is the combination which it exhibits of structural features, some of which are unique, while others are individually characteristic of widely different genera or species of Teleosts.

The extension of the air-bladder from its normal position in the abdominal region into the tail is by no means of infrequent occurrence in Teleosts, although it may take place in various ways. In some species (*e. g.*, species of *Exocœtus*) the organ is prolonged backwards without undergoing subdivision into the expanded hæmal canal of the anterior part of the tail (**11**. p. 222). In others the caudal extension takes the form of an unsymmetrical prolongation of the entire organ along the left side of the tail, as in *Ophiocephalus*, or along the right side, as in the Characinoid *Alestes Hasselquistii*, C. & V. (*A. dentex*, Müll. & Trosch.) [**11**. p. 222] *, and in the Siluroids *Cryptopterus micronema*, Blkr., and *C. micropogon*, Blkr. (**2**. pp. 202–3). More frequently, perhaps, the air-bladder subdivides anteriorly to the first caudal hæmal arch, and in the form of two bilaterally-arranged cæcal prolongations extends for a variable distance on either side of the tail and internal to the lateral caudal musculature, as in some Sparidæ, Scombridæ, and Carangidæ (**11**. pp. 221–2), and also as in *Notopterus*. But in none of the Teleosts above mentioned, except *Notopterus*, or in any others with which I am acquainted, do the caudal prolongations of the air-bladder exhibit the slightest tendency to branch, or to develop structures in any way comparable to the singular fringe of bifurcate ventral diverticula which are so characteristic of *Notopterus borneensis*; and very rarely in any Teleost are the

* On the authority of Cuv. & Val.

inner walls of the caudal cæca reduced to so attenuated a condition through the intimacy of their relations and attachments to the caudal skeleton, as is the case in the last-mentioned species. Even in the two species of *Cryptopterus*, where the caudal portion of the air-bladder is in contact with the subvertebral hæmal arches and spines, the walls of the organ are of uniform thickness and are quite free from any special connection or attachment to the skeleton.

Perhaps, on the whole, the air-bladder of certain species of Sparidæ (*e. g.*, species of *Box*) approaches more nearly to that of *Noptopterus* than does the bladder of any other Teleosts. In *Box vulgaris*, C. & V., not only are caudal cæca present, but the inner or mesial walls of these structures are devoid of an outer fibrous coat, or tunica externa, and the tunica interna, which alone remains, closely invests the opposite sides of the hæmal arches and spines of the caudal vertebræ. The resemblance is further heightened by the fact that in *Sparus salpa*, L. (*Box salpa*, C. & V.), as Weber (12. p. 71 *et seq.*) pointed out, auditory cæca are also present, although in the location of their connection with the auditory fontanelles and in some minor details the latter Sparoid does not precisely agree with *Notopterus*. On the other hand, *Box* has no bifurcate ventral diverticula in connection with the caudal cæca, and the air-bladder is wholly destitute of internal septa, and of a ductus pneumaticus in the adult.

The extension of the air-bladder into the tail in *Notopterus*, as no doubt is also the case in many other Teleosts, is to be associated with the extreme shortness and laterally-compressed shape of the abdominal portion of the body, which, if the bladder is to acquire its normal degree of development as a hydrostatic organ, necessitates its prolongation into the caudal region *.

In the disposition of the internal septa, and especially in the development of a principal longitudinal septum which, anteriorly, meets an incomplete transverse septum, the cœlomic or abdominal portion of the air-bladder of *Notopterus* presents some approximation to the characteristic T-shaped arrangement of the primary septa in the bladder of a considerable number of Siluroids; and the resemblance is rendered still more marked by the fact that in both the carinate shape of the suprajacent axial skeleton involves a partial subdivision of the anterior portion of the bladder through the inpushing of its dorsal wall in the

* See reference to remarks by Günther (7. footnote to p. 491).

median line. On the other hand, however, *Notopterus* differs from the more typical Siluroids in the absence of the transverse septum on the right side, the unsymmetrical division of the air-bladder by the longitudinal septum, and also in the fact that it is the basioccipital which is carinate ventrally and not, as in Siluroids, the confluent centra of the "complex" vertebra.

An additional resemblance to many Siluroids is also apparent in the tendency of the outer fibrous coat of the air-bladder to become invaded by ossific deposit whenever it becomes attached to, or inserted into, adjacent portions of the axial skeleton. The bony ridges which bound the basioccipital grooves for the reception of the auditory cæca, and the squamous hinder portions of the prootics which form the outer walls of the bony culs-de-sac wherein these cæca terminate, almost certainly owe their existence to the ossification of the tunica externa at the points where it is attached to these cranial bones.

By no means the least noteworthy of the many interesting structural features in connection with the air-bladder of *Notopterus borneensis* is the extreme shortness and relatively wide calibre of the ductus pneumaticus, and the position of its œsophageal aperture in close proximity to the last pair of branchial clefts. Such a combination of features is eminently characteristic of the Acipenseroid, Crossopterygian, Amioid and Lepidosteoid Teleostomi and of the Dipnoi, but is rarely to be found in Teleosts, although an approximation thereto may be noted in such genera as *Arapaima*, *Heterotis*, and *Gymnarchus*, at any rate to the extent that in these Teleostei the ductus is both short and wide.

In the absence of gas-secreting or gas-absorbing "red glands" and "red bodies," *Notopterus* agrees with the generality of those Teleosts in which an open ductus pneumaticus is retained throughout life.

From a physiological point of view, the most noteworthy feature in the air-bladder of *Notopterus* is its intimate relation with the auditory organ.

The presence of antero-lateral cæcal outgrowths from the air-bladder is by no means uncommon in Teleostean Fishes, especially in the Sparidæ, Sciænidæ, Cottidæ, and Gadidæ; and such outgrowths may even extend so far forwards as to become more or less closely related to the skull, but it is only in a comparatively limited number of genera that the air-bladder acquires any special connection or physiological relationship with the auditory organ. As regards the precise nature of the connection between the two organs in different Fishes, three principal methods may be distinguished:—

A. Auditory cæca are present, and the anterior extremity of each is closely applied to a fontanelle in the outer wall of the auditory capsule, the utricular portion of the membranous labyrinth and the surrounding perilymph being in relation with the inner surface of the fibrous membrane by which the fontanelle is closed. In no part of their course are the auditory cæca enclosed within bony canals or grooves, and no connection between the auditory organs of opposite sides of the head has so far been described.

According to Stannius (**11.** p. 171) this method of connection is characteristic of *Priacanthus* * *macrophthalmus*, C. & V. (*P. arenatus*, C. & V., or *P. cruentatus*, C. & V. †), among the Serranidæ; of certain species of Berycidæ pertaining to the genera *Myripristis* and *Holocentrum*; and possibly of *Hyodon claudulus* (*H. tergisus*, Les.), the solitary representative of the North-American freshwater family of the Hyodontidæ. Jeffery Parker (**8**) has recorded an essentially similar arrangement in the New Zealand Gadoid, *Lotella* (*Pseudophycis*) *bacchus*; and Weber (**12.** pp. 71–72) for such Sparidæ as *Sparus salpa*, Linn. (*Box salpa*, C. & V.), and *S. sargus*, Linn. (*Sargus Rondeletii*, C. & V.).

B. Instead of being closed by a fibrous membrane, the auditory fontanelles are open, and through each of them passes a cæcal diverticulum from the corresponding utriculus, which thus becomes directly and closely applied to the anterior extremity of an auditory cæcum.

Those Teleosts which afford examples of this method of connection by direct apposition are also characterized by certain other noteworthy modifications. Thus, for the greater part of its forward course each slender auditory cæcum is enclosed in bone, first traversing a groove and subsequently a canal in the exoccipital bone, and finally terminates by dividing into two distinct vesicular enlargements, of which one lies in a chamber excavated

* The generic name "*Triacanthus*" given by Stannius (*loc. cit.*) is apparently a misprint for *Priacanthus*.

† For synonyms of *P. macrophthalmus*, *vide* Brit. Mus. Cat. Fishes, 2nd ed. vol. i. p. 353 & p. 356.

in the pterotic bone and has no special relations with the auditory organ. The other vesicle occupies a globose chamber in the prootic, and there becomes closely applied to the wall of the corresponding utricular diverticulum, which enters the chamber through an auditory fontanelle in the prootic. In some instances there appears also to exist a connection between the two utriculi in the form of a transverse sub-cerebral canal, which, however, is not to be regarded as homologous with the similarly situated ductus endolymphaticus of the Cyprinoid and Siluroid Teleosts. Such a utricular connection was first discovered in *Clupea harengus* by Weber (**12.** p. 77), and subsequently by Breschet (**1**) in *C. alosa*. On the other hand, the evidence as to the existence of a supra-cerebral connection between the two sacculi, as affirmed by Hasse (**6**), or between the two utriculi, as stated by Breschet (**1.** p. 17), is too conflicting to admit of any definite conclusion being drawn *.

The preceding arrangement, which appears to be restricted to the physostome family of the Clupeidæ, was first described by Weber in the Herring (*Clupea harengus*). Recently, Ridewood (**9.** p. 26) has contributed an excellent revision of the anatomical relationships of the two organs in the six British species of Clupeidæ, viz.:—*Clupea harengus*, Linn., the Pilchard (*C. pilchardus*, Walb.), the Sprat (*C. sprattus*, L.), the Allis Shad (*C. alosa*, L.), the Thwaite (*C. finta*, Cuv.), and the Anchovy (*Engraulis enchrasicholus*, Cuv.). These species apparently include all the Clupeidæ in which a connection between the auditory organ and the air-bladder has so far been described.

C. In a third and last series of Teleostean fishes, viz., the physostome families of the Cyprinidæ, Characinidæ, Siluridæ, and Gymnotidæ, the connection between the air-bladder and the auditory organ attains its maximum complexity and physiological importance, and is effected, not by auditory cæca, but by means of a chain of movable Weberian ossicles. The auditory organs of opposite sides of the head are connected together by the mesial union of the two endolymphatic ducts, one from each sacculus, and the consequent formation of a transverse sub-cerebral connection between the two sacculi. From the point of union of the two ducts a median sinus endolymphaticus, enclosed in a similar median extension of the perilymphatic spaces of the

* For a discussion of this point, *vide* Ridewood (**9.** pp. 38–39).

two auditory capsules (sinus impar), is prolonged backwards to its physiological connection with the most anterior of the series of Weberian ossicles *.

Whether *Hyodon claudulus* is rightly to be regarded as an example of the first method, as stated above, or not, is by no means quite clear. The description of the connection between the auditory organ and air-bladder in this Teleost, as given by Stannius (*op. cit.* p. 171), is as follows:—

"Bei *Hyodon claudulus*—und ganz analog verhält sich *Notopterus*—communicirt das vordere Ende des Schwimmblasenkörpers durch enge Oeffnungen mit zwei sphärischen dickwandigen Blasen. Jede derselben legt sich in eine Vertiefung der Knochen der Hinterhauptsgegend ihrer Seite und haftet eng an den letzteren. Dem vordersten Theile jeder dieser Blasen entspricht eine Oeffnung in den Knochen, die inwendig von einem Theile des Vestibulum, auswendig aber von der innersten Haut dieser Blase bekleidet ist, indem die weisse Faserhaut derselben im Umkreise der äusseren Gehörsöffnung aufhört und nicht über letztere selbst sich fortsetzt."

From this account it would seem that, as in the Clupeidæ, the auditory fontanelles in *Hyodon* are not closed by fibrous membranes, and, consequently, the auditory cæca, after losing their outer fibrous coat, are either closely related to the vestibular walls, or in actual contact therewith, or, at all events, are not separated by any intervening fibrous membrane. If, however, the description given by Stannius is correct, then the statement "und ganz analog verhält sich *Notopterus*" is scarcely applicable to that Teleost, inasmuch as there is no doubt as to the existence of a separating membrane in *Notopterus*.

It would be interesting to ascertain if any tubular communication between the two vestibuli, similar to that present in the Clupeidæ, exists also in *Hyodon*. So far as I am aware, no observations on this point have yet been made.

Comparison of *Notopterus* with the various Teleosts mentioned above, proves that it furnishes an additional example of the first of the three methods by which the air-bladder and auditory organ are brought into physiological relationship, although in one or two minor features an approach to the second type is indicated.

Thus in *Notopterus* there is no direct contact between the

* For references *vide* Bridge & Haddon (**2**. p. 65 *et seq.*).

walls of the utriculi and those of the auditory cæca, the two structures being separated by the membranes which close the auditory fontanelles; neither is there any open tubular communication between the utricular and saccular portions of the auditory organs of opposite sides of the head by means either of sub-cerebral or supra-cerebral connections. In these features *Notopterus* closely agrees with those Teleosts in which the first method has been adopted. On the other hand, it is equally evident that to some extent *Notopterus* approaches the second type and resembles the Clupeidæ in the fact that, for a part of their course, the auditory cæca are enclosed in bony grooves and for the terminal portion of their extent occupy the interior of bony culs-de-sac, and also in the origin of the cæca from an anterior tubular portion of the air-bladder.

It is perhaps worth remarking that some little variation in minor details exists amongst those Teleosts which offer examples of the first and second methods, more especially with regard to the precise position of the auditory fontanelles and the nature of the cranial or periotic bones which form their boundaries, and also in the degree of tenuity of the closely related walls of the auditory prolongations of the air-bladder.

For example, in *Sparus* (*Box*) the fontanelle is represented by Weber (12. tab. vii. fig. 62) as being situated posteriorly to the foramen for the exit of the Vagus nerve. In *Pseudophycis bacchus* the auditory fontanelle is described by Parker (*loc. cit.*) as situated between the basioccipital and the opisthotic, and immediately beneath the Vagus foramen. In *Holocentrum spiniferum*, Gthr., the fontanelle is bounded by the exoccipital, opisthotic, and prootic bones, and is anterior to the Vagus foramen; and in *Notopterus*, as we have seen, the prootic, opisthotic, and basioccipital encircle the fontanelle. Finally, in the Clupeidæ the fontanelle is a simple perforation in the prootic alone, and hence is more anteriorly placed than in any other Teleosts. There can be no doubt, I imagine, that the precise location of the fontanelle and the nature of its limiting bones, are due to the varying extent to which the auditory cæca are prolonged forward, and perhaps also to variations in the size of the fontanelle itself.

Of much more importance is the degree of tenuity of the walls of the auditory cæca at their point of contact or closest relationship with the auditory organs; for upon this will depend the degree of intimacy and perfection of the physiological connection between the two organs.

On this point it may be mentioned that in *Pseudophycis bacchus,* as described by Parker (*op. cit.*), the anterior extremity of each auditory cæcum forms a thickened pad which is closely applied to the membranous sheet closing the corresponding auditory fontanelle. From this account it may be legitimately inferred that both the outer fibrous coat of the cæcum and the tunica interna are applied to the fontanelle and its membrane. In *Sparus* (Weber, *op. cit.*), on the contrary, the tunica externa of the auditory cæcum ceases at the margins of the fontanelle, and only the extremely thin tunica interna is applied to the membrane which closes the aperture. So far as this point is concerned *Notopterus* closely resembles *Sparus*; but in the Clupeidæ, and possibly in *Hyodon*, the connection of the two organs becomes even more intimate, inasmuch as it is effected by the actual apposition of the limiting walls of auditory cæca and utricular outgrowths.

The derivation of the second and more intimate type of connection between the air-bladder and the auditory organ from the first method is easy to imagine, as the process simply involves the atrophy of the fibrous membranes closing the auditory fontanelles, so as to admit of the actual contact of the two organs by the direct apposition of outgrowths from each. A much more difficult problem is the genesis of the third method by means of Weberian ossicles, and so far no satisfactory solution has yet been offered. There is every probability, however, that the Weberian mechanism has been independently evolved, but that the initial stages of its evolution have not yet been discovered, if they exist, in any Fishes at present living.

In his account of the connection between the air-bladder and auditory organ in *Pseudophycis bacchus*, Parker (*op. cit.*) remarks: "The anterior end of the air-bladder fits closely against the hinder end of the skull and is produced outwards into paired pouches which are in contact with the thin skin beneath the operculum and in front of the shoulder-girdle." To this arrangement *Notopterus* offers a parallel in the close relation of the auditory cæca to the cæcal diverticula of the branchial cavity, and, therefore, to the external medium in which the fish lives. The Siluroids (2) also afford examples of a somewhat similar modification. In the majority of these Teleosts the lateral walls of the anterior chamber of the air-bladder are in contact, often over a considerable area, with the superficial skin behind the pectoral girdle.

Notopterus is by no means the only Teleost in which the existence of cranial fontanelles, more or less closely associated with the auditory organ, has been recorded. Nevertheless, the position of these vacuities, and their precise relation to the membranous labyrinth, exhibit a wide range of variation in different Teleosts.

In *Notopterus*, as we have seen, the fontanelles are situated on the upper surface of the hinder part of the skull and immediately dorsad to the auditory capsules.

According to Stannius (**11.** p. 170) cranial fontanelles essentially similar to those of *Notopterus* exist also in *Hyodon claudulus*.

In the Herring (*Clupea harengus*, L.) "the ventro-external surface of the sacculus lies over a membranous fenestra of the skull-wall, situated between the exoccipital, basioccipital, and prootic bones, and described by several authors as a foramen ovale; the sacculus-wall is here separated from the mucous membrane of the mouth by this membrane only" (Ridewood, *op. cit.* p. 38).

In referring to certain of the Macruridæ, Stannius (*op. cit.* p. 170)* states :—" Bei *Lepidoleprus trachyrhynchus* † findet sich seitlich am Hinterkopfe über dem oberen Ende der Kiemenspalte eine trichterförmige von dünner Haut gesschlossene Grube, welche in den zur Aufnahme des Gehörorganes bestimmten Theil der Schedelhöhle hineinragt. Zwischen der Innenfläche ihrer Haut und dem Labyrinthe liegt eine faserig-gallertartige Substanz." Similar fontanelles are said to be present in *L. cœlorhynchus*, but not in *L. norvegicus*.

The skin-covered fontanelles on the postero-superior surface of the skull of *Mormyrus* somewhat resemble those of *Lepidoleprus*, except that immediately beneath the external skin there is a perfectly free and very thin lamina of bone which partially covers each fontanelle (Stannius, *op. cit.* p. 170 ‡). Fontanelles,

* On the authority of Otto, Tiedemann u. Treviranus' Zeitschrift f. Physiol., Bd. ii. S. 86

† =*Macrurus trachyrhynchus*, Risso.

‡ Apparently on the authority of S. Heusinger, Meckel's Archiv f. Anat. u. Physiol. 1827, Bd. i. S. 324.

similar to those of *Mormyrus*, are also said to be present in *Gymnarchus niloticus* (Stannius, *l. c.* *).

Mention may also be made of the prevalence of median fontanelles in the cranial roof in many Siluroids, although in these Fishes the structures in question have no special relation to the auditory capsules †.

It is certainly worthy of remark that the existence of cranial fontanelles, as a possible avenue for the transmission of sound vibrations from the water to the auditory apparatus, has been recorded not only for those Fishes in which the air-bladder has no connection with the membranous labyrinth (e. g., *Mormyrus*, *Macrurus*), but also, and apparently quite as frequently, even in those Teleosts in which such a connection is known to exist (e. g., *Clupea*, *Hyodon*, and *Notopterus*).

IX. Remarks on the supposed Auditory Function of the Air-bladder.

The physiological value of the connection between the air-bladder and the auditory organ is still one of the unsolved problems of comparative physiology, and this statement seems to be equally applicable to any of the three principal methods by which such a connection is established. The reason for this is, no doubt, that practically nearly all attempts to solve the problem have been based upon anatomical evidence alone; and, as must be admitted, morphological data are often unreliable, and even misleading, when employed as the sole basis for physiological deductions, and not infrequently appear to support with remarkable impartiality conclusions of a widely different character. When the problem has received the attention of the experimental physiologist, then, and then only, may a final and satisfactory solution be expected.

The question has been most frequently discussed in connection with the Ostariophyseæ ‡, and, so far, comparatively little attention has been devoted to those Teleosts (e. g., *Sparus*, *Notopterus*, *Hyodon*, *Clupea*, &c.) in which the connection of the air-bladder and auditory organ is effected by other means than the presence of Weberian ossicles. In venturing to discuss certain physio-

* According to Erdl, see Stannius, *l. c.*, footnote to p. 170.

† Professor Howes has reminded me of the large lateral occipital fontanelles in the Cyprinidæ (*c.f.* Sagemehl, Morph. Jhb. Bd. xvii. p. 495).

‡ The physostomous families of the Cyprinidæ, Siluridæ, Characinidæ, and Gymnotidæ, in which a Weberian mechanism is present.

logical points in connection with the latter Fishes, I must again emphasize my conviction that physiological conclusions drawn solely from anatomical data must be regarded as little more than tentative and provisional suggestions.

At the conclusion of his account of the mode of connection between the air-bladder and the auditory organ in certain species of *Sparus*, Weber (*op. cit.* p. 72) states his views as to the physiological value of the connection in the following words:—

"Prima utilitas hæc est, ut tremoros soniferi aquæ toti piscium corpori communicati, a vesica natatoria elastica recipianter, in se colliquantur, et in membranam, fenestram vestibuli ossei obducentem, transferantur, cuius tremoros liquorem, cavum cranii replentem, movent itaque vestibulem membranaceum ipsum, ab aqua cranii circumdatum, afficiunt ad quam quidem utilitatem vesica natatoria, quippe quæ singulis costis affixa est, aptissima videtur."

On this theory the air-bladder, by reason of its connection with the auditory organ, becomes a physiological accessory to audition, in addition to its usual and normal function as a hydrostatic organ.

In discussing Weber's view of the auditory function of the air-bladder and Weberian ossicles in the Ostariophyseæ, it was pointed out by Bridge and Haddon (**2**. p. 276) that, assuming sound-waves to be transmitted from the air-bladder to the auditory organ by these ossicles, the fact that such stimuli would, in the first instance, affect certain median and unpaired structures common to both auditory organs (sinus impar and sinus endolymphaticus) involved the difficulty that the membranous labyrinths of opposite sides of the head would be affected with equal intensity and simultaneously, and, consequently, as no differential stimulation took place, the Fish would be incapable of appreciating the direction of the sound.

Sörensen (**10**. pp. 185–186), in attempting to mitigate the force of this criticism, remarks:—"As far as I can see this is the only real objection that can be made against the theory of Weber. But I do not judge it to be of great importance. If this objection were absolutely valuable, no human being would be able to decide if a sound arises before or behind him when the direction of the sound coincides with the symmetrical plane of the body; and this, however, we are able to decide. And, would not this objection be just as valuable if you presume the sound not to be transmitted to the ear through the air-bladder? Are not the Fishes deprived of the means by which the higher Vertebrata are able to judge the direction of the sound, viz., by turning the head (or external ears) to the right or to the left? It must also be kept in mind that it is always very difficult thoroughly to understand that beings differently conditioned know how to use the powers with which they are endowed, especially when these powers are inferior to those bestowed upon us."

Sörenson's attempt to lessen the importance of what he terms the only "real objection" to Weber's theory does not impress one as being very successful. The capacity for appreciating the direction of sounds, whether employed as a means of securing prey, or escaping from enemies, or, as in the case of gregarious Fishes, as a means of keeping together in shoals for breeding or other purposes, must be of primary importance in any modification of the auditory organ in the direction of giving to its possessor exceptional powers of hearing. Fishes may have no power of rotating or inclining the head, but it must not be forgotten that a slight deflection of the long axis of the body to the right or left will at once enable the differential action of the two auditory organs to come into play, and the Fish would be in a position to appreciate the direction from which the sound is travelling. An Ostariophysean, in so far as those parts of the auditory apparatus which it possesses in common with all other Fishes are concerned, is in much the same position as regards the sense of direction. It is quite true that the two auditory organs are in open communication by means of a sub-cerebral transverse ductus endolymphaticus; but it is also obvious, I think, that the auditory organ, right or left, turned towards the direction of the sound, will be stimulated appreciably sooner, or it may be more forcibly, than its fellow, and hence the cognizance of direction. Again, is it not possible, or even probable, that sound-waves reaching the auditory organs simultaneously by two distinct channels will have their effect nullified, and the sense of direction seriously interfered with? In fact it seems extremely probable that sound stimuli which, according to Weber's hypothesis, are received by the auditory organs through the air-bladder and Weberian ossicles, would have the effect of confusing any sense of direction based upon similar stimuli, generated by the same cause and at the same moment, but pursuing, as in the generality of Fishes, the usual direct path through the bones and other structures of the head to the membranous labyrinths. It may be also urged that this objection loses none of its force when it is considered that the cranial bones are far more pervious to sound-waves travelling in water than, as is the case with terrestrial animals, in air.

If this argument has any force, does it not suggest that the Weberian mechanism, considered as an accessory to audition, may prove a positive disadvantage to the Fish in so far as the sense of direction is concerned? Finally, if the Weberian mechanism is a means of increasing the acuteness of the sense of hearing, is it not a little remarkable that sounds heard through this agency convey no idea of direction, especially when the latter is of so much importance to the animal, and that the sense of direction should depend upon the perception of sounds of an obviously more limited range of intensity which reach the auditory organs directly through the head?

Other objections which may be urged against Weber's theory as applied to the Ostariophyseæ are scarcely pertinent to the present discussion, which is designedly restricted to those Fishes in which there is no Weberian apparatus and the auditory organ and air-bladder are connected by other methods.

It may at once be affirmed that the same "real objection" is equally applicable to such Fishes as *Notopterus*, *Sargus*, *Sparus*, *Hyodon*, *Clupea*.

In some of these Fishes (e. g., *Sparus*, *Sargus*, and *Clupea*) there is no longitudinal bipartition of the air-bladder, which, therefore, for the greater part of its extent encloses a simple undivided cavity. Sound-waves in the gases of the air-bladder travelling along the auditory cæca will ultimately affect the auditory organs to an equal extent and simultaneously. Hence, these Fishes will derive no sense of direction from auditory stimuli reaching the membranous labyrinths by such channels. Whatever sense of direction they possess will be derived from those stimuli which reach the auditory organs by the usual path through the skull; but here, as in the Ostariophyseæ, we are confronted with the probability that such sense of direction will be interfered with by the stimuli received through the air-bladder.

From this point of view the condition of the air-bladder in *Notopterus* is especially significant. For more than three-fourths of its extent the organ consists of two lateral chambers; and if, by an anterior extension of the longitudinal septum, these compartments had become entirely separated from each other, and each had remained continuous with the auditory cæcum of its side, it is at least conjecturable that each chamber would be somewhat differently affected by sound-waves impinging on its own side of the body and eventually propagated to the auditory organ of the same side. In this way, it seems possible that stimuli received by the auditory organ through the intervention of the air-bladder might be competent to give rise to a sense of direction. So far, however, from this being the case, the longitudinal septum ceases at the very point where its forward prolongation seems to be most desirable; and, in consequence, the auditory cæca arise from an anterior, median, tubular portion of the bladder, which is only slightly divided longitudinally by the carinate growth of the suprajacent axial skeleton. Hence, as in non-septate air-bladders, sound-waves are propagated to the auditory organs simultaneously and with equal intensity.

There is also another point which deserves consideration in discussing the possible auditory function of the air-bladder in these Fishes.

Well-marked cranial fontanelles are present in several of them, and these structures are not only paired but each is in immediate relation with the auditory organ of its side of the head. Do not these skin-closed fontanelles afford a better channel for the transmission of sound-vibrations to the membranous labyrinths than the air-bladder?, and is not one of these structures somewhat superfluous if we regard both of them as sound-transmitting organs? Moreover, so far from interfering with the sense of direction, cranial fontanelles would probably facilitate the differential action of the two auditory organs.

If the connection of the air-bladder with the auditory organ is not subservient to the sense of hearing, can any other function be assigned to it?

In the case of the Ostariophyseæ, Ramsay Wright (13) and Bridge and Haddon (2) have supported the view that the connection of the two organs was possibly for the purpose of enabling these Fishes to appreciate the varying degrees of tension of the gases in the air-bladder, resulting from corresponding variations of hydrostatic pressure produced by locomotor movements involving differences of depth. Subsequent reflex or voluntary impulses, it was suggested, might find expression in the exercise of some form of regulatory control over the liberation of gas through the ductus pneumaticus, so that only so much gas will be eliminated as will suffice to maintain the Fish in a plaue of least effort.

In attempting to extend this theory to such Teleosts as *Sargus*, *Hyodon*, *Priacanthus*, *Notopterus*, and *Clupea*, it must be at once admitted that there are grave difficulties in the way. It is easy to conceive how distension or contraction of the air-bladder, produced by variations in the superincumbent column of water, would be competent to give rise to stimuli affecting the auditory organ. A tendency to over-distension may be conceived to produce such a bulging of the anterior extremities of the auditory cæca as would modify the condition of the perilymph surrounding the auditory organs, and impart a stimulus to the sensory epithelium of those organs. The objection to this view is, however, that it is very difficult to see in what way the contingent efferent impulses will find expression. In Fishes like *Notopterus* and *Clupea*, where a ductus pneumaticus is present, the existence of some kind of regulatory control over the liberation of gas from the air-bladder is possible; but this suggestion is obviously inapplicable to such Fishes as, for example, the species of *Sparus* and *Sargus* in which the ductus atrophies in the adult. In the latter genera, variations in the amount of gas present in the air-bladder must depend upon the relatively slow processes of gaseous secretion or absorption; and it is at least within the bounds of conjecture that the connection of the air-bladder and auditory organ forms part of a reflex mechanism by which the varying tensions of the gases of the air-bladder constitute a stimulus to the auditory organ and central nervous system, and, ultimately, by reflex action lead to such a modification of the rate of secretion or absorption as will vary the amount of gas in the bladder in accordance with the requirements of the Fish. The special advantage to the Fish may be that secretion and absorption will take place more rapidly than is the case where pressure-stimuli have no special means of affecting a sensory organ, and adjustment to varying hydrostatic pressures effected with greater promptitude. Nevertheless, it must be acknowledged that there is at present but very little evidence, either physiological or anatomical, which can be adduced in support of these suggestions.

Admitting, however, the want, or rather the paucity, of evidence for such tentative suggestions, is it not possible that the connection of the auditory organ and the air-bladder may have to do with a simpler physiological rôle? The danger which a Fish incurs from over-distension of the air-bladder as the result of a too rapid rise in the water to the reduced pressure of a higher level has been emphasized elsewhere (2); and, without involving any alteration in the rate of gaseous absorption, the afferent impulses communicated to the auditory organ may, through appropriate efferent channels, lead to such modifications of the locomotor movements as will enable the Fish to guard against over-distension, and return to its normal plane of equilibrium or "least effort" at a greater depth.

It is a significant illustration of the difficulties of the problem that even Weber, who was primarily responsible for the theory of the auditory function of the air-bladder in those Fishes in which that organ is connected with the membranous labyrinth, was sufficiently far-seeing to admit the possibility of a second function. Immediately following the quotation with reference to *Sparus*, which has been previously given, Weber proceeds (12. pp. 72–73):—

"Altera vesicæ natatoriæ utilitas hæc est, ut aëre vesicæ compressione alvi in appendices superiores impulso, membranaque fenestram utramque vestibuli ossei obducente tensa et introrsum pressa, aqua cranii cavum replens adeoque vestibulum membranaceum, ad hac aqua circumdatum ipsum prematus.

"Quam ob rem, si cranio aperto et labyrintho membranaceo conspicuo vesica natatoria manu comprimatur, facile hic vesicæ natatoriæ contractæ effectus oculis percipitur. Per vesicam enim manu compressam liquor cranium replens non solum propellitur, sed vestibulum membranaceum ipsum quoque motu liquoris cranii commovetur."

The two paragraphs just quoted suggest that Weber certainly entertained the idea of the air-bladder being the means of conveying to the auditory organ stimuli due to its varying degrees of distension, such as, we may presume, are naturally brought about by variations of depth and, therefore, of pressure; and, further, prompt the remark that the term "Weberian theory" may be as reasonably applied to this view as to the "auditory theory" with which the name is more generally associated.

In conclusion, it may be affirmed that there are obvious objections both to the auditory and hydrostatic views of the physiological *raison d'être* of the connection between the air-bladder and the auditory organs, which, in the present state of our knowledge of the individual functions of those organs, cannot easily be explained away in accordance with either theory. With a more precise and definite acquaintance with the physiology of the organs in question, and a more extended knowledge of the habits and mode of life of the Fishes concerned, it is possible that some definite conclusions may be arrived at; but the final solution of the problem must rest with the experimental physiologist.

Whatever the significance of the inter-relationship of the air-bladder and the auditory organ, there can be no question as to its physiological importance. Such a connection presents varying degrees of perfection and specialization in different Teleosts, and its independent evolution in widely different families seems to suggest the possibility that it is correlated with the requirements of special or local conditions of life, and, while attaining its maximum development in the dominant families of freshwater Teleosts *, is nevertheless present in simpler forms in a limited number of both freshwater and marine Fishes.

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XI. EXPLANATION OF THE PLATES.

Plate 36.

Fig. 1. Lateral view of the left branchial cavity, to show the relation of its anterior cæcal extension to the left auditory cornu of the air-bladder. The operculum and pectoral girdle have been removed. (Nat. size.)

Fig. 2. View of the interior of a portion of the left caudal prolongation of the air-bladder. The outer wall of the bladder has been partly removed and partly reflected above and below. A portion of the outer wall of a ventral diverticulum has also been cut away in order to show one of the ventral series of vacuities. (Nat. size.)

Fig. 3. Lateral view of the anterior and abdominal portions of the air-bladder. The outer wall of the left half of the bladder, except that portion of it which is traversed by the oblique transverse groove between the sub-spherical sac and the abdominal part of the organ, which has been left as a narrow oblique strip, has been removed, so as to show the longitudinal septum throughout its entire ength. The outer wall of the left auditory cæcum has been removed, and the œsophagus and ductus pneumaticus laid open. (× 2.)

Plate 37.

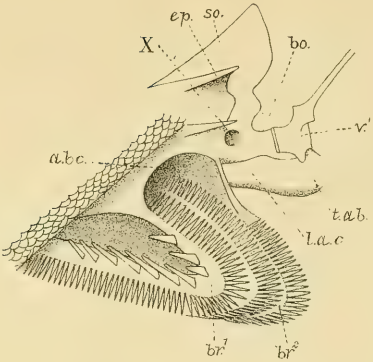
Fig. 4. Lateral view of the posterior portion of the right side of the skull. (× 2.)

Fig. 5. View of the interior of the hinder part of the right half of the cranial cavity, as seen in a vertical longitudinal section of the skull. (× 2.)

Fig. 6. Supero-lateral view of the posterior portion of the right side of the skull. (× 2.)

Reference letters.

a.b.c. Anterior diverticulum of the left branchial cavity.
ab.p. Abdominal portion of the air-bladder.
a.f. Auditory fontanelle.
als. Alisphenoid.
a.p. Accessory articular process for the centrum of the first vertebra.
b.g. Basioccipital groove.
bc. Basioccipital.
br^1, br^2. First and second branchial arches.
c.f. Cranial fontanelle.
c.s. Entrance to bony cul-de-sac.
d.p. Ductus pneumaticus.
d.v. Dorsal vacuity.
d.w. Dorsal wall of the air-bladder.
e.o. Exoccipital.
e.p. Epiotic.
f. Frontal.
f.c. Filiform cæca.
g. Lateral groove for the sensory canal of the head.
h.s. Hæmal spine.
l.a.c. Left auditory cæcum.
l.c.c. Left caudal cæcum of the air-bladder.
l.p. The inpushed dorsal wall of the tubular portion of the bladder.
l.s. Longitudinal septum in the abdominal part of the bladder.
l.s'. Longitudinal septum in the subspherical sac.
œs. Œsophagus.
o.g. Oblique groove separating the subspherical sac from the abdominal part of the bladder.
op. Opisthotic.
p. Parietal.
pro. Prootic.
ps. Parasphenoid.
pt. Pterotic.
r.a.c. Aperture leading to right auditory cæcum.
r.e. Radial or interspinous element of anal fin.
sb.s. Subspherical sac.
spo. Sphenotic.
so. Supraoccipital.
tp. Tubular portion of the air-bladder.
ts. Transverse septum.
u.s.r. Utriculo-saccular recess in the basioccipital.
v'. First vertebra.
v.d. Ventral diverticulum.
v.v. Ventral vacuity.
X. Foramen for the exit of the Vagus nerve.



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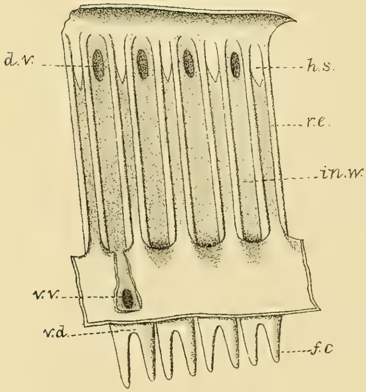

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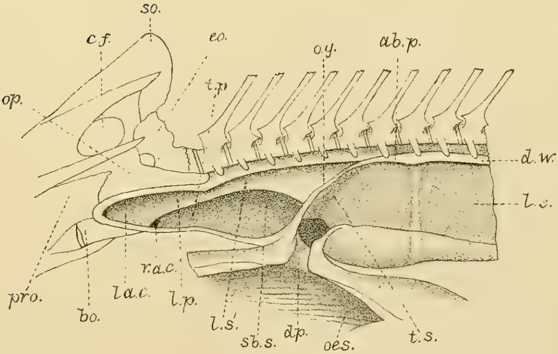

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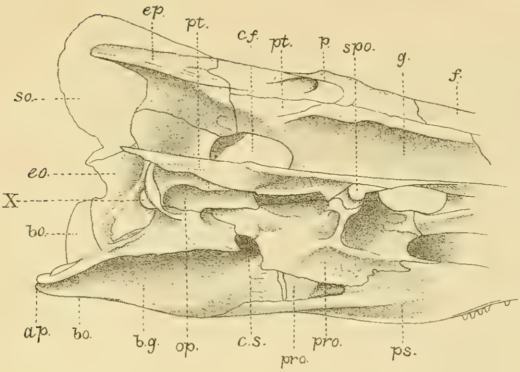
M. P. Parker lith.

Geo. West & Sons imp.

NOTOPTERUS BORNEENSIS.



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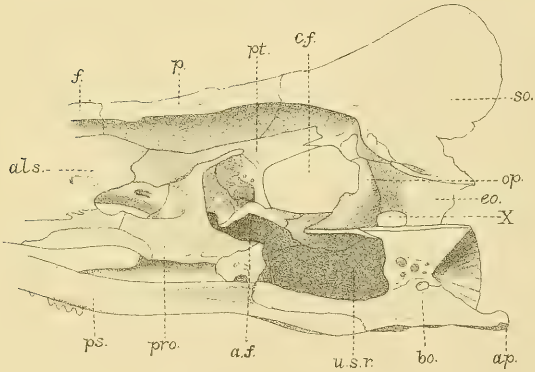

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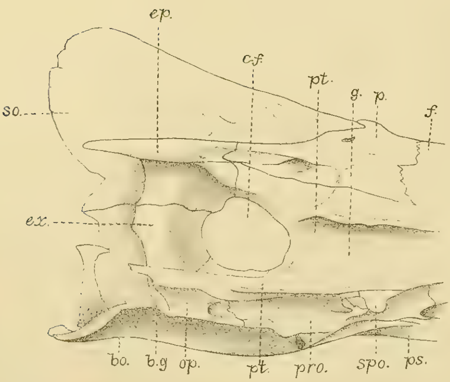

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